



Demographic Characteristics of a Maine Woodcock Population and Effects of Habitat Management



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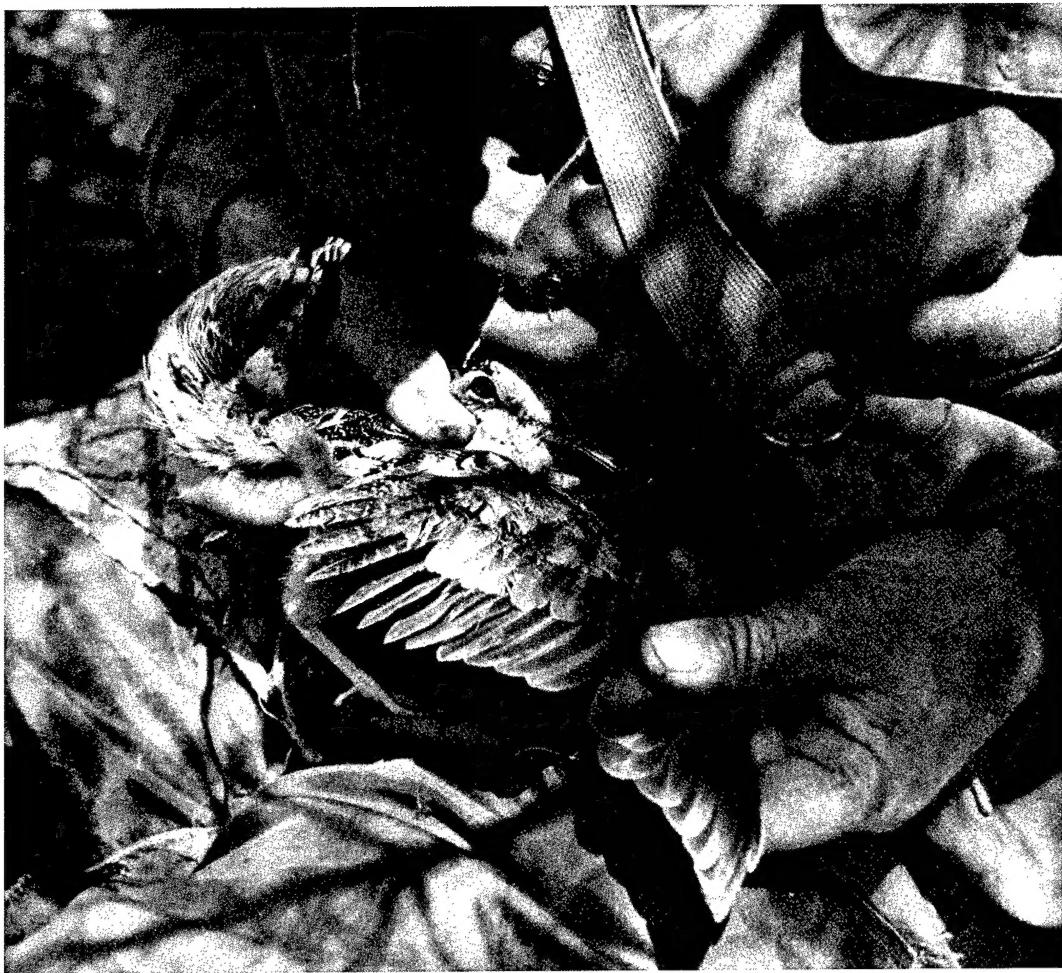
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An adult female American woodcock (*Scolopax minor*) captured with a brood. *Photo by G. M. Haramis.*

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by

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Abstract

A population of American woodcock (*Scolopax minor*) was studied on a 3,401-ha area of the Moosehorn National Wildlife Refuge in northeastern Maine from 1976 through 1985. During 1976-83, from 4 to 64 clearcuts were created each year, opening up large contiguous blocks of forest. A combination of mist nets, ground traps, nightlighting techniques, and trained dogs were used to capture and band 1,884 birds during the first 5 years. Capture and recapture data (totaling 3,009 observations) were used with both demographically closed and open population models to estimate population size and, for open population models, summer survival. Flying young, especially young males, represented the greatest proportion of all captures; analysis showed that young males were more prone to capture than young females. Male courtship began about 24 March each year, usually when there was still snow in wooded areas. Males ≥ 2 years old dominated singing grounds during April each year, but this situation changed and first-year males dominated singing grounds in May. Singing males shifted from older established singing grounds to new clearcuts soon after we initiated forest management. Many males were subdominant at singing grounds despite an abundance of unoccupied openings. Three hundred adult females were captured and, except for 1978, the majority were ≥ 2 years old. The year in which female

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homing rate was lowest (1979) was preceded by the year with the largest number of 1-year-old brood female captures and a summer drought. Summer survival of young was lowest in 1978 and was attributed to summer drought. The year 1979 had an abnormally cool and wet spring, and was the poorest for production of young. Capture ratios of young-to-adult females obtained by nightlighting could be used to predict production on our study area.

Closed population model estimates did not seem to fit either young or adult data sets well. Instead, a partially open capture-recapture model that allowed death but no immigration seemed to fit best. Only the number of males in the population changed significantly during the study. An increase from 88 males in 1976 to 156 in 1980 was attributed to habitat management. Singing-male surveys on our area detected little change in the number of singing males, but our independent population estimates from mark-recapture data showed a larger total male population by 1980. Annual density estimates for all age and sex classes ranged from 19 to 25 birds/100 ha. A hypothesis on the breeding system of the American woodcock is presented as well as a discussion of management implications, including the importance of creating high-quality habitat on private lands.

The American woodcock (*Scolopax minor*) is a popular migratory game bird throughout eastern North America. Unfortunately, lack of adequate sampling of woodcock hunters leads to rather imprecise and probably biased national estimates of the annual harvest of this bird. There is no question, however, that the number of woodcock hunters has increased over the last two decades (Martin 1979). Most recent estimates indicate that more than 2 million birds are harvested by hunters each year (Tautin et al. 1983).

At the same time that harvest indices for woodcock have increased, spring population indices have decreased in the eastern part of the species' range (Tautin et al. 1983). Several workers have speculated or provided evidence that land-use trends influence woodcock populations (Cushwa et al. 1977; Dobell 1977; Coulter and Baird 1982; Gutzwiller et al. 1982; Dwyer et al. 1983). In the most recent study (Dwyer et al. 1983), changes in spring woodcock abundance in the northeastern United States were correlated with changes in specific habitat types over a 10-year period. Specifically, an increase in urban and industrial area was significantly related to the call-count index decline in a sample of woodcock routes from nine northeastern States. These results indicate the importance of describing changes in local woodcock abundance as they relate to habitat changes.

The literature on the American woodcock is extensive and has been summarized twice over the last decade. Reeves (1975) included many general woodcock citations in a larger annotated bibliography of all webless migratory game birds, and Dwyer et al. (1979) provided 462 scientific citations for this species from 1927 to 1978. Seven symposia and workshops dealing with the ecology

and management of the woodcock have also been held since 1966. Despite these many studies and publications, there are few long-term studies from specific study areas. Mendall and Aldous (1943), Liscinsky (1972), Whitcomb (1974), and Gregg (1984) are notable exceptions.

In 1976, we began a long-term study on the Moosehorn National Wildlife Refuge, Maine, to develop techniques for woodcock habitat management that could be used by small landowners or commercial forestry operations (Sepik et al. 1977; Sepik and Dwyer 1982). We were also interested in evaluating the woodcock singing-ground survey, determining the age and sex structure of a woodcock population and how this structure changes between years, and assessing the response of a local population to habitat management. A special effort was made during the first 5 years (1976-80) to estimate woodcock population numbers through intensive banding and recapture programs. We then continued singing-male captures through 1982 and singing-male censuses through 1985.

The present paper presents characteristics of the woodcock population on the Moosehorn refuge from 1976 to 1985. Specifically, we provide data on (1) population size, (2) population age and sex structure, (3) breeding-male behavior, (4) production, (5) the relation between singing-ground surveys and actual population size, and (6) the response of the local population to habitat management.

Study Area

Concerns about a declining woodcock population led to the establishment of the Baring Unit of the Moose-

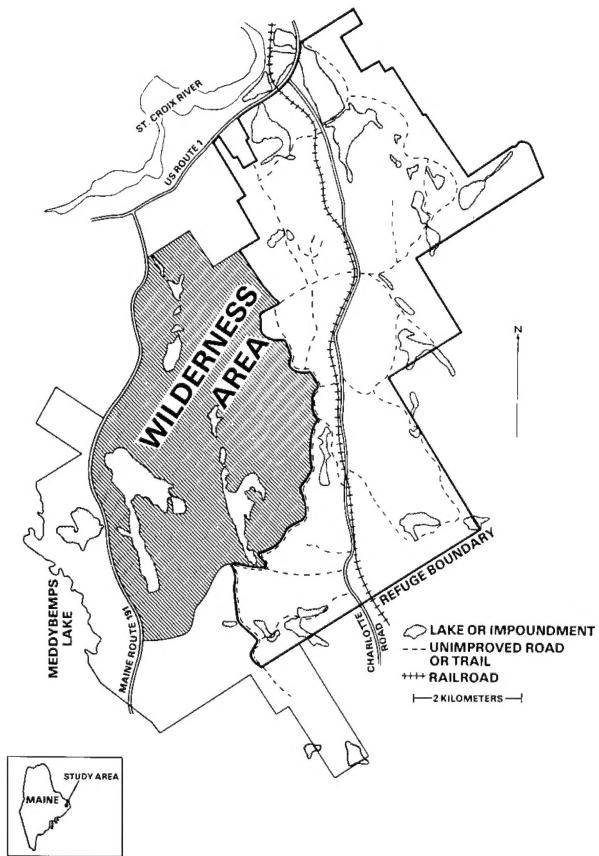


Fig. 1. Location of study area in northeastern Maine. Bold line indicates the actual 3,401-ha study area within the Moosehorn National Wildlife Refuge.

horn National Wildlife Refuge in 1937. The refuge is located in northeastern Maine on the Canadian border in the primary woodcock breeding range (Fig. 1). Much of the land in the refuge was clearcut and burned by wildfire about the turn of the century. At the same time, many of the farms that were economically tied to the forest industry were abandoned as the timber supply declined and mechanization increased.

By 1975, most of the 6,580 ha of refuge land was covered by a mature, second-growth forest interspersed with natural and man-made water bodies, several meadows, and managed blueberry (*Vaccinium* spp.) fields. The forest was composed of pure stands of spruce (*Picea* spp.) and balsam fir (*Abies balsamea*) in the early stages of a spruce budworm (*Choristoneura fumiferana*) infestation. Hardwood stands dominated by birch (*Betula*

spp.), red maple (*Acer rubrum*), and aspen (*Populus* spp.) were common and were gradually being replaced by conifers. Alder (*Alnus* spp.) stands were common along streams and in some abandoned fields. Less than 150 ha of forest land had been harvested since the inception of the refuge.

We selected, for our study, the eastern part of the Baring Unit (Fig. 1) that contained most of the better woodcock habitat on the refuge. We did not include the 1,895-ha Wilderness Area in the study because it was closed to habitat management, there was limited access to the area, and surveys before 1976 indicated that very few woodcock were present. The Wilderness Area contained mature stands of both hardwoods and conifers with few forest openings that were attractive to woodcock.

Table 1. Number of clearcuts on the Moosehorn National Wildlife Refuge, 1976-83.^a

Type of clearcut	Year							
	1976	1977	1978	1979	1980	1981	1982	1983
Block	6	3	1	9	29	0	9	1
Strip	7	10	12	26	26	11	0	3
Other ^b	0	2	8	19	9	0	1	0
Total	13	15	21	54	64	11	10	4

^aIncludes all cuts made during a calendar year. Late summer and fall cuts would not be available to breeding birds the first year.

^bIncludes large (up to 24 ha) salvage cuts.

In 1976, a limited, small-scale woodcock habitat management program was initiated. Over the next 3 years, small clearcuts (0.4 ha each) were created in a variety of cover types. The techniques proved promising and a large-scale harvesting program was started in 1979. Under this program, larger clearcuts were made in the form of blocks (2 ha) and strips (0.2-0.4 ha) at a rate of 40 to 60 ha/year (Sepik and Dwyer 1982). Other clearcuts, some as large as 24 ha, were created in spruce-fir stands in an attempt to salvage timber damaged by spruce budworm. Four to 64 clearings were created each year from 1976 to 1983, resulting in many openings of varied sizes in what were once large contiguous blocks of forest (Table 1; Fig. 2).

Methods

Singing-male Survey

Singing-male American woodcock were counted by a technique similar to that used in the annual Federal survey (Clark 1970), with the following changes: (1) route length varied (between 0.5 and 4.5 km in this survey versus 5.8 km in the Federal survey), (2) census stops were closer together (0.5 km in this survey versus 0.64 km in the Federal survey), (3) survey routes were not selected at random, but covered the entire study area, and (4) all singing grounds were located on a map to ensure that all courting males were counted. All routes within the study area were censused once each year. Some routes were censused on foot where no road system existed. A typical annual survey involved about 20 routes (142 stops) that were surveyed during the period (25 April-15 May) recommended for the annual rangewide survey (Clark 1970).

Capture Techniques

Singing Males

Singing males were captured with mist nets (Sheldon 1967) placed around courting locations during the last week in March through the first week in June. A singing ground was first observed and the location and flight path of the male was noted. On a subsequent evening, two to five 3 × 10-m mist nets were placed on the singing ground. Peripheral nets were used to capture any females or subdominant males present on the area. Males were classified as dominant or subdominant (Godfrey 1974) on the basis of behavior. A male in possession of a singing ground was defined as a dominant male. Subdominant males were those that either vocalized (peented) on the periphery of a singing ground or were caught later in the evening after the capture of the dominant male. We were able to determine dominant versus subdominant males because an observer was always present at each singing ground watching bird activity during capture periods.

Broods

Woodcock broods were located each year by searching all likely brood habitat in forest stands, along fields and clearcut edges, roadsides, and alder covers, with one or more pointing dogs (Ammann 1974, 1977). When a brood was located, we attempted to capture the hen as well as the chicks. All broods were presumed to consist of four chicks, unless careful searching proved otherwise. Broods with fewer chicks were purposely recontacted within 2 days to make sure no chicks were overlooked.

Summer Field Captures

Woodcock used blueberry fields, pastures, hayfields,

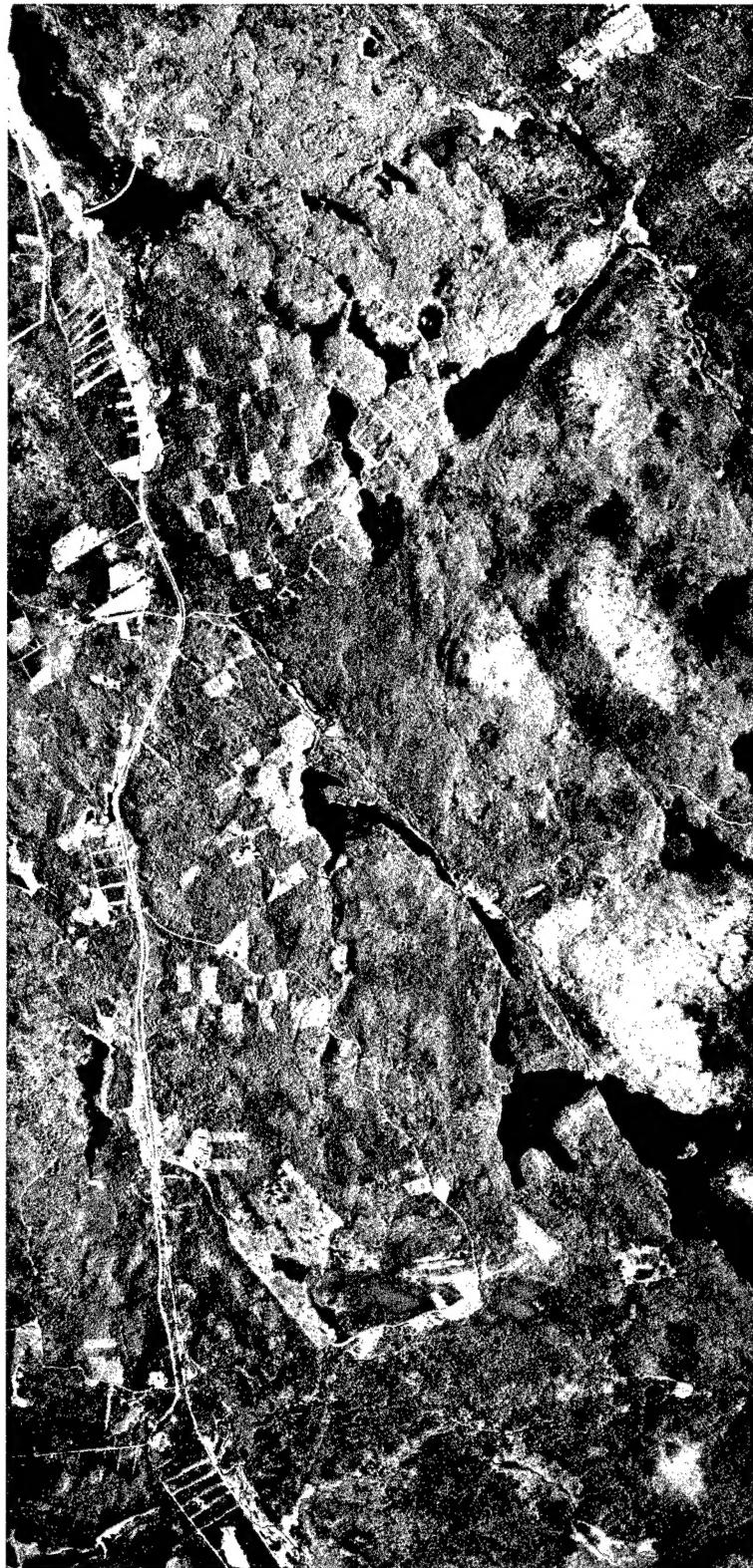


Fig. 2. The location and pattern of clearcuts in 1983 within the study area.

and clearcuts for nocturnal summer roosting. Seven to 12 of these areas with a history of woodcock use were netted weekly with 9 to 25 mist nets depending on the size of the field. Net configurations were changed each week to keep birds from becoming familiar with net locations. These areas, plus a few other areas too large to effectively use mist nets, were nightlighted (Rieffelberger and Kletzly 1967) during rainy, overcast nights. Nightlighting was accomplished by three or more persons either walking through roosting fields or driving in fields in a four-wheel drive vehicle. We located birds on the ground using a quartz iodine light powered by a 12-V battery and netted them with a long-handled hoop net. If a bird flushed, it was followed with the light until it landed and was captured or until it left the field.

Trap Lines

From the first week in June to the last week in August each year, woodcock were caught in their diurnal covers with modified shorebird traps (Liscinsky and Bailey 1955). Nine traplines of 6 to 23 traps each were located in early successional growth, usually alder covers. Traps were constructed by clearing an area of vegetation about 80 cm wide and 5 to 15 m long, then placing a 30-cm high chicken wire lead down the center. A cloverleaf cell, made of 2.5 × 5.0-cm mesh wire and covered by nylon netting, was placed at both ends of the lead or at both ends and at the center of the lead in the case of longer trap sites. Woodcock entered a trap cell through a funnel-type entrance that also prevented them from escaping.

Age and Sex Determination

Sex of adults and fledged young was determined by width of the outer 3 primaries (Greeley 1953). Wing characteristics (secondary feather patterns) were used to separate fledged young from adults; adult males and females were classified as 1 year old or second-year (SY) and ≥ 2 years old or after-second-year (ASY; Martin 1964). Bill length measurements allowed age determination of chicks in a brood (Ammann 1974, 1982). Weight and bill length measurements were taken on all adults, fledged young, and chicks throughout the study.

Population and Survival Estimation

Singing-male woodcock numbers can be indexed by a call-count survey (Mendall and Aldous 1943; Tautin et al. 1983) which is used to derive a rangewide index of woodcock numbers. Singing-male surveys were used

in this study to obtain an index of singing males, but actual numbers of adults and fledged young in the summer population were estimated by mark-recapture techniques.

Open Population Estimation Methods

We estimated population numbers for each age and sex class using the demographically open population model of Jolly (1965) and the partially open model of Darroch (1959). With the Jolly (1965) model, population gains and losses are allowed to occur between sampling periods through birth and immigration and death and emigration. The Darroch (1959) model allows only losses between sampling periods. We believed that this variation was appropriate because capture data were separated by age and sex groups and the capture period for young birds took place after most recruitment to the population had occurred. We also believed that there was little immigration over spring-summer. Goodness-of-fit tests (chi-square) were calculated for both the Jolly (1965) and Darroch (1959) model estimates when data were sufficient according to the method of Jolly (1982). When open population models are appropriate, they have the added advantage of providing survival rate estimates for capture intervals.

For the open population model analysis we divided the 20-week adult capture session beginning in early April each year into five capture periods. The 10-week capture session for young beginning in mid-June each year was divided into three to five capture periods each year. Generally low capture probabilities and our belief that it took several weeks to adequately trap the entire area necessitated use of a small number of capture periods.

Closed Population Estimation Methods

We were unsure whether our study would allow strict adherence to the assumptions necessary for demographically closed population estimates. Our capture sessions for adults and young were too long to support an assumption of negligible mortality. We do believe, however, that neither emigration nor immigration was a problem for the adult data sets. This is supported by recent telemetry studies (Sepik, unpublished data) on the same area. Results of closure tests from the Otis et al. (1978) models were not totally reliable because statistical tests to assess closure are confounded by behavioral responses to trapping (Otis et al. 1978). An animal that becomes trap-shy and uncatchable becomes indistinguishable from one that dies or emigrates. Estimates from closed population models were never-

theless calculated because we wished to make comparisons with estimates from the open or partially open population models, we wished to test for unequal capture probabilities in the population, and we believed mortality might be the only closure violation.

White et al. (1982) provided a computer program and goodness-of-fit tests for the series of closed population models detailed in Otis et al. (1978). They also provided a discriminant function to objectively select the appropriate model (and thus the appropriate catchability assumptions) for any data set. The simplest of these models are Model M_0 (constant probability of capture), Model M_t (capture probabilities vary with time or trapping occasion), Model M_b (capture probabilities vary because of behavioral response to initial capture), and Model M_h (capture probabilities vary by individual animal). Other more complicated models dealing with various combinations of the above models are theoretically possible (e.g., M_{th} —time and heterogeneity are present) but estimators are available (Otis et al. 1978) only for M_{bh} (behavioral response and heterogeneity).

We separated the total capture time into 15 periods for adults and 8 periods for young. In general, closed population models have fewer data requirements than open population models, so we could use a larger number of capture periods. Data were entered separately for each age and sex class.

Results and Discussion

Woodcock Captures

Total captures of all new birds for all years was 1,884 (Table 2). The fewest new birds were captured in 1976

(310) and the most in 1978 (473). Of the total, 11.3% were adult (ASY and SY) females, 14.0% were adult males, 17.6% were flightless young, 23.7% were fledged young (HY) females, and 33.4% were HY males.

Different capture methods did not produce equal proportions of birds in each age and sex class (Table 3). Furthermore, there was year-to-year variation in the numbers caught by each method. The year-to-year variation can be most easily explained by prevailing environmental conditions, that is, most capture methods depend to a large degree on atmospheric moisture conditions. Nightlighting, for instance, is most effective on moonless, overcast nights during light rain (Rieffenberger and Kletzly 1967). This is confirmed in that higher numbers of birds were captured by this method in 1976, 1977, and 1979 when the most precipitation occurred (June–August precipitation was 36.7, 33.2, and 24.7 cm, respectively; 26-year average = 23.3 cm). Conversely, ground trapping tended to be relatively more effective during dry conditions, such as in 1978 when June–August precipitation was only 9.8 cm.

There were differences in the number of birds in each age and sex class caught by each method regardless of year-to-year variation (Table 3). Most adult males were captured in mist nets at singing grounds; smaller numbers were caught by other methods during the rest of the year. Adult males characteristically are the least likely to be caught in summer roosting fields because they undergo most of their postnuptial wing molt from June through August (Owen and Krohn 1973) and are apparently less mobile than other age and sex classes at that time. Fewest adult females were captured in mist nets (Table 3). Females are more difficult to catch with

Table 2. *New captures of American woodcock (Scolopax minor), by year and by age and sex class, on the Moosehorn National Wildlife Refuge, 1976–80.*

Year	Age and sex class					Total
	Adult ^a male	Adult ^a female	Young ^b male	Young ^b female	Flightless young	
1976	53	30	153	74		310
1977	40	54	141	105	85	425
1978	44	54	153	129	93	473
1979	75	40	94	65	61	335
1980	52	35	89	73	92	341
Total	264	213	630	446	331	1,884

^aIncludes ASY and SY.

^bHY.

Table 3. Summary of captures of American woodcock (*Scolopax minor*) by capture method, year, and age and sex, on the Moosehorn National Wildlife Refuge, 1976-80.^a

Year	Mist net				Nightlighting				Ground traps				Dogs ^b					
	Adult ^c male	Adult		Young male	Young female	Adult male	Adult		Young male	Young female	Adult male	Adult		Young male	Young female	Adult female	Flightless young	Total
		male	female	male	female		male	female	male	female		male	female	male	female			
1976	31(29) ^d	6	46	26	15	16	56	30	7	8	51	18	—	—	—	310		
1977	42(38)	7	28	22	10	25	76	42	10	21	37	41	22	85	468			
1978	56(52)	15	79	52	8	15	31	26	10	23	43	51	22	93	524			
1979	82(77)	17	37	21	17	28	32	27	4	11	25	17	10	61	389			
1980	79(70)	14	44	29	2	9	19	19	6	10	26	25	21	92	395			
Total	290(266)	59	234	150	52	93	214	144	37	73	182	152	75	331	2,086			

^aIncludes first captures each year of banded birds from previous years (returns).

^bCaptured with a hand net with the aid of a pointing dog.

^cAdult = both ASY and SY.

^dNumber in parentheses is the number of males caught on singing grounds.

Table 4. *Woodcock chicks recaptured as flying young during the same year, on the Moosehorn National Wildlife Refuge, 1977-80.*

Sex	1977(85) ^a	1978(93)	1979(61)	1980(92)	All years (331)
Male	19	10	16	12	57
Female	18	21	7	9	53

^aNumber in parentheses is the total number of chicks captured in a given year.

mist nets than are males because they do not perform courtship flights. Most were captured with dogs or in ground traps.

Fledged young represented the greatest proportion of all captures (Table 2). Young males predominated in total captures each year as in previous studies (Sheldon 1961; Kletzly and Rieffenberger 1969; Gregg 1984). Our data from the Moosehorn National Wildlife Refuge are unique because we banded a large sample of flightless young for 4 years; many were recaptured and sexed after they had fledged (Table 4). If one assumes equal sex ratio at hatching and no sex differential survival to fledging, it is possible to test whether the first capture of flying young birds is biased to either females or males. In 1977, equal numbers of males and females were recaptured from our original sample of banded chicks. In 1978, recaptures were skewed toward females, and in 1979 and 1980, the reverse was true. During all 4 years, more young males than young females were recaptured from the original banded sample of chicks but differences were not statistically significant (Dwyer et al. 1982).

We also examined the proportion of flying young caught more than once in any given year and tested for differences between sexes using a chi-square test (1 df/year). All young caught by all capture methods were used in the analysis. We found no significant difference between the proportion of young males and young females that were captured more than once (1976, $P = 0.71$; 1977, $P = 0.38$; 1978, $P = 0.63$; 1979, $P = 0.45$; 1980, $P = 0.44$).

In summary, assuming an equal sex ratio at hatching and equal sex-specific survival, there is yearly variation in the sex-specificity of capture probability for HY woodcock with an overall indication that young males are initially more catchable than young females. However, young males are not captured more frequently than young females after the initial capture. Differences in opinion exist as to whether ease of capture (Dunford and Owen 1973) or nocturnal habitat use (Sheldon 1967; Gregg 1984) is responsible for the preponderance of captured males.

Singing Males

Chronology

Singing-male activity usually began around 24 March each year. Usually some snow remained in wooded areas at that time. During years of prolonged snow cover or late spring storms, woodcock were observed courting on the snow and on frozen ponds. However, when evening temperatures were above 0°C, courtship activity generally took place.

We began capturing singing males each year about 1 April. At this time most traditional singing grounds were occupied and evening temperatures usually were above freezing. By the last week in May, at least one dominant male woodcock had been caught at most of the singing grounds on the study area. Courtship activity usually ended during the first week in June.

Age Ratios

The overall, yearly age ratio (ASY:SY) of dominant male woodcock caught on singing grounds from 1977 through 1982 showed little variation from year to year and no trend ($r = -0.34$, $P > 0.05$; Table 5). However, when the age ratio of dominant males caught during the first half of the breeding season (1 April-28 April) was compared with that of males caught during the second half (29 April-26 May), there was a significant difference (paired t -test, $t = 2.99$, $P < 0.05$). Older males (ASY) dominated the singing grounds during April (1.33 ASY:SY), but the ratio changed in favor of the younger males (SY) in May (0.72 ASY:SY). Whitcomb (1974) noted a similar trend in Michigan.

More than 50% of the males caught on singing grounds during early April from 1977 to 1982 had been banded in previous years (Table 6). It appears that returning ASY males are among the first woodcock to reach the area or that SY and migrant males, unfamiliar with the area, are unwilling or unable to make use of the vacant singing grounds. As the breeding season progressed, more unbanded, dominant males were captured (Table 6). When the original males ceased

Table 5. *Age ratios (ASY:SY) of male woodcock during four periods, spring through summer, 1977-82.*

Period	Year						Mean
	1977	1978	1979	1980	1981	1982	
1 April-28 April	1.0	1.5	1.64	1.24	1.11	1.5	1.33
29 April-26 May	1.0	0.45	0.45	0.80	1.0	0.6	0.72
1 April-26 May	1.0	1.0	0.92	1.03	1.09	0.79	0.97
1 June-1 September	0.71	0.64	0.61	0.50	0.50	0.17	0.52

courting or were killed by predators they were probably replaced by subdominant males.

The summer age ratio (0.52 ASY:SY) was significantly less (paired *t*-test, $t = 5.56$, $P < 0.05$) than the age ratio of males caught during the first half of the breeding season (Table 5). Unless survival rates in the spring vary between male age classes, the summer age ratio should be similar to the spring age ratio. The difference in the early spring ratio of courting males suggests that older males either arrive earlier or are more successful in defending their territories against younger males, or both. This relation disappears during the second half of the breeding season.

Age ratios of courting males also varied according to the type of singing ground. There was significantly greater use of newly created clearcuts (the first year after cutting) by SY males (0.90 ASY:SY, paired *t*-test, $t = 2.98$, $P < 0.05$). Older clearings were favored by ASY males (1.33 ASY:SY; Table 7).

Subdominant Males

The presence of nondisplaying males at active singing grounds has been firmly established (Sheldon 1967; Godfrey 1974; Ellingwood 1983; and others). The actual role that these males assume during courtship is not clear. Sheldon (1967) described them as opportunistic breeders and Godfrey (1974) referred to them as "ancillary," that is, behaviorally subordinate birds that are forced into a subdominant, nonterritorial role by the dominant male. Subdominant males replace display-

ing males upon removal of the dominant bird (Modafferi 1967; Sheldon 1967; Godfrey 1974; Ellingwood 1983).

During 1978-82, 33 subdominant males were captured on the periphery of occupied singing grounds or after the capture of a dominant male. The overall seasonal age ratio revealed that SY birds predominated (0.38 ASY:SY) in the subdominant male population. Differences in age ratio of subdominant males between April (0.53 ASY:SY, $N = 23$) and May (0.11 ASY:SY, $N = 10$) were nonsignificant ($\chi^2 = 2.16$, 1 df, $P > 0.05$). In contrast to Modafferi (1967), we found significant differences in the age ratio of dominant and subdominant males captured in April ($\chi^2 = 4.18$, 1 df, $P < 0.05$) indicating age-related dominance during the first half of the breeding season. Subdominant-to-dominant male capture ratios (regardless of age) exhibited no change between April and May ($\chi^2 = 1.46$, 1 df, $P > 0.05$) suggesting that a portion of the male population remains subdominant even late in the season and may not have an opportunity to breed.

Eight (24.2%) of the subdominant males were recaptured as dominant males during the same breeding season. The distance these birds moved averaged 1.3 km (range, 0-2.7 km), with four males moving >1.8 km. The shift from subdominant to dominant status may occur more often than we noted because we generally mist netted an active singing ground only once during a breeding season.

Table 6. *Return ratios (unbanded:previously banded) of dominant male woodcock caught on singing grounds by 2-week period, 1977-82.*

Male birds	1 April-14 April	15 April-28 April	29 April-12 May	13 May-26 May
Return ratio	0.97	1.30	2.0	2.0
<i>N</i>	67	85	66	54

Table 7. *Age ratio (ASY:SY) of dominant male woodcock on clearcuts and traditional singing grounds.*

Clearing type	1977	1978	1979	1980	1981	1982	Mean
Clearcut	1.25	0.44	0.67	1.07	1.29	0.69	0.90
Traditional	1.17	1.36	1.08	1.33	1.63	1.42	1.33

Singing-ground Fidelity

The degree of fidelity to a singing ground (based on 60 dominant males caught 2 or more years on a singing ground) indicated that 30% used the same area and 95% were within 1.5 km of the original singing ground (Table 8). Similar results were reported by Sheldon (1967) for Massachusetts birds and Godfrey (1974) for Minnesota birds.

Male fidelity to an area seemed to be limited to older woodcock. Only 39% of the ASY males caught as dominants on a singing ground were new captures. The rest had been captured previously as courting males or sometime during a previous summer. However, 76.4% of the SY dominant males were new captures (Table 9). We estimate that 50% of the HY males produced on the study area were captured and banded during spring and summer each year (Table 10). We have no evidence that the probability of surviving, returning to our area, or being caught is different between banded and unbanded birds. Therefore, we would expect about 50% of the SY dominant male population to be banded. Because the actual figure is about 20%, we believe that young woodcock disperse widely during their first year. Owen and Morgan (1975) reported that juvenile woodcock ranged twice as far as adults during summer and Gregg (1984) showed that indirect band recoveries of young woodcock were much more widely distributed than adult recoveries.

Individual male woodcock also seemed to have an affinity for certain types of singing grounds. Of the 61 males encountered on different singing grounds in successive years, most moved either from one clearcut

to another or from one established site to another (Table 11).

Weight Changes

We found no significant weight changes for male woodcock during the courtship season. Both SY and ASY male weights were lowest at about the midpoint of the breeding season (Table 12). Marshall (1982) reported a similar trend for Minnesota woodcock. Both age classes exhibited the same trend in weight change and there was no difference (paired *t*-test, $t = 0.68$, $P > 0.05$) between the weight of dominant ASY and SY males. Weights of subdominant males also did not differ significantly from dominant males (paired *t*-test, $t = 0.70$, $P > 0.05$). Similarly, Keppie and Redmond (1985), in a removal study, found no difference in weights of singing-ground occupants (dominants) and replacement males (subdominants). Factors other than courtship activity apparently affect male body weight in spring.

Mendall and Aldous (1943) reported that severe spring weather can cause mortality in returning spring migrants, presumably because of starvation due to earthworm scarcity. Should conditions be less severe but still stressful, one would expect weight loss to occur. The late April-early May weight loss noted here may be the result of earthworm scarcity. Rabe et al. (1983) found a positive relation between both soil moisture and temperature and earthworm abundance in the upper soil strata. In a 1-year study in Michigan they found low earthworm biomass during late April. We suspect that annual variation in spring environmental conditions may result in earthworm scarcity and subsequent woodcock weight loss in some years.

Table 8. *Fidelity of courting male woodcock previously captured on a singing ground and recaptured 1 or more years later on a singing ground.*

Male birds	Distance (km) between successive captures							
	0	0-0.3	0.3-0.6	0.6-0.9	0.9-1.2	1.2-1.5	1.5-1.8	>1.8
Number	18	9	10	9	6	5	2	1
Percent	30	15	17	15	10	8	3	2

Table 9. *Age and capture status (new or previously banded) of dominant male woodcock captured on singing grounds, 1978-82.*

Year	ASY			SY		
	New	Return ^a	New (%)	New	Return	New (%)
1977	11	8	57.9	9	7	56.2
1978	4	19	17.4	18	5	78.3
1979	19	17	52.8	33	8	80.4
1980	12	26	31.6	21	10	67.7
1981	12	13	48.0	17	4	80.9
1982	5	12	29.4	20	1	95.2
Total	63	95	39.5	118	35	76.4

^aCaught during a previous year.

Table 10. *The estimated portion of the population of young male woodcock that were captured and banded, 1976-80.*

Year	Number of young males banded	Young male population ^a estimate	Young males banded (%)
1976	153	263 ± 35 ^b	58.2
1977	141	271 ± 43	52.0
1978	153	259 ± 45	59.1
1979	94	199 ± 42	47.2
1980	89	254 ± 80	35.0
Total	630	1,246 ± 23	50.3

^aBased on the Darroch (1959) model.

^b± SE.

Table 11. *Movement of courting males caught during 2 or more years.*

Period	Number moving between singing ground types			
	Clearcut to clearcut	Clearcut to established	Established to clearcut	Established to established
1976-82	13	3	7	38

Table 12. Weight in grams (\pm SE) of dominant and subdominant male woodcock caught on singing grounds. Number in parentheses is sample size.

Date	Dominant		
	ASY	SY	Subdominant
1-7 April	134.6 (16) \pm 2.9	139.5 (8) \pm 6.8	141.6 (5) \pm 4.0
8-14 April	135.4 (25) \pm 2.1	137.0 (19) \pm 2.4	140.8 (10) \pm 6.8
15-21 April	136.0 (33) \pm 2.3	137.2 (17) \pm 3.4	134.8 (5) \pm 8.8
22-28 April	139.7 (17) \pm 4.2	137.3 (23) \pm 2.6	136.5 (2) \pm 3.0
29 April-5 May	130.0 (8) \pm 5.8	131.5 (15) \pm 2.7	121.0 (1)
6-12 May	133.8 (22) \pm 2.6	135.8 (30) \pm 2.3	135.0 (4) \pm 6.5
13-19 May	137.1 (14) \pm 3.1	138.1 (23) \pm 2.9	152.0 (2) \pm 30.1
20-26 May	140.1 (11) \pm 5.1	141.1 (8) \pm 6.1	141.0 (2) \pm 8.5
27 May-2 June	151.2 (6) \pm 9.5	150.0 (6) \pm 8.9	153.0 (1)

Singing-ground Availability and Use

In spring 1976 there were only seven small clearcuts in the study area. Most male woodcock were singing in blueberry fields, reverting farmland, hayfields, natural openings, or other areas. Twelve different males were caught on one 2.5-ha blueberry field and as many as four males were heard singing there at one time.

Gradually, as the number of clearcuts increased, we noted a shift away from some types of established sites to these new openings (Table 13). The large blueberry field that attracted four males in 1976 had only one dominant male in later years and the percentage of males using blueberry fields declined from 1977 to 1982 (Table 13) even though all blueberry fields were maintained by periodic burning.

The use of hayfields, abandoned fields, and natural openings varied between years but did not show a sharp decline in use. At the beginning of the study, more than

30% of the singing males used roads, pasture or meadowland, and areas along the railroad tracks. These "other" areas (Table 13) did show a decline in use.

Singing grounds were categorized as preferred singing grounds (used 3 or more consecutive years), periodic singing grounds (used during only 2 consecutive years), and sporadic singing grounds (used occasionally but never for 2 consecutive years). Several blueberry fields, natural openings, hayfields, and abandoned fields showed relatively constant use. Clearcuts showed the highest preferred use, second highest periodic use and the highest sporadic use (Fig. 3). We attribute the high sporadic use to the great number of clearings developed over the course of the study. Singing males had a large number of clearcuts from which to choose and thus moved from one clearcut to another among years. Also, regeneration on many clearcuts was rapid, precluding extended use.

Table 13. Type of clearings used by courting male woodcock, 1977-82.

Year	Clearing type											
	Clearcut		Blueberry field		Hayfield		Abandoned field		Natural forest opening		Other	
	N	(%)	N	(%)	N	(%)	N	(%)	N	(%)	N	(%)
1977	9	26	7	20	1	3	3	9	3	9	12	34.2
1978	13	25	9	17	4	8	4	8	5	10	14	28.5
1979	25	33	7	9	5	11	10	13	9	12	13	18.8
1980	25	35	4	6	5	7	4	6	7	10	20	30.7
1981	16	36	3	7	3	6	6	14	4	9	12	27.3
1982	22	55	5	13	1	2	2	5	2	5	8	20.0

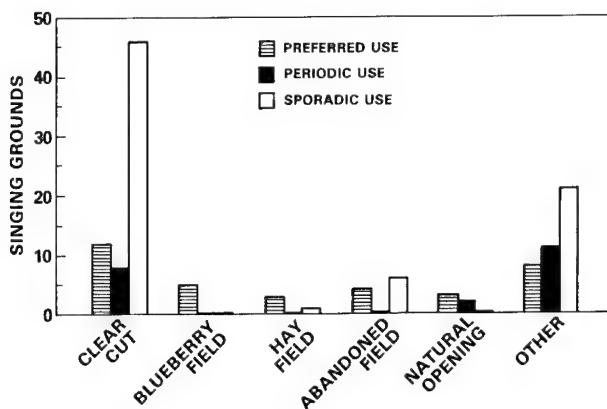


Fig. 3. Singing-ground use by clearing type.

The spatial distribution of singing males in the later years of our study reflected the distribution and increasing number of clearcuts. In 1976 singing males were found along the railroad track running north-south through the study area, in blueberry fields in the east-central part of the study area, and along the road system in the northeastern part of the area (Fig. 4). By 1980 concentrations of birds still occurred along the railroad track but more birds were clumped in the northeastern part of the area (Fig. 5) where many strip and block cuts had been established. In 1985, the year with the highest singing-male count ever recorded, many more birds were using the northeastern part of the area (Fig. 6) because of the creation of larger block cuts (Fig. 2).

In 1981, a warm March resulted in an early migration. On 17 March about 50 cm of snow fell and remained on the ground for nearly 2 weeks. We noted a 32% decline from the previous year in the number of courting males. Likewise, the number of courting males remained low in 1982, probably because of a 7 April blizzard that dropped 25–50 cm of snow on much of the northeastern United States. During these 2 years the use of clearcuts by courting males continued to increase (Table 13).

We doubt that the shift by some birds to clearcuts was caused by a decline in the quality of established singing grounds because most of these sites had changed very little over the course of the study. Many of the singing grounds recorded by Mendall and Aldous (1943) were still in use at the beginning of the present study. The new clearings were apparently more attractive to courting males than some types of established sites.

Female Population Structure

We did not capture enough females on singing grounds to give a yearly breakdown of the spring age ratio. However, of the 25 females captured on singing grounds from 1977 through 1982, 13 were ASY and 12 were SY. This was not significantly different from the age ratio of females caught during summer (1.02 ASY:SY ; $\chi^2 = 0.057$, $P > 0.75$; Table 14). Eighty females were caught with broods during the same period. Except for 1978, the majority of females were ASY and the age ratio averaged 1.9 ASY:SY, but was equal to or greater than 3.0 ASY:SY for 2 of these years. The overall age ratio of brood females was different from the age ratio of adult females captured during summer ($\chi^2 = 8.94$, $P < 0.005$). Apparently, females of both age classes bred, but the older females were more successful in hatching a clutch.

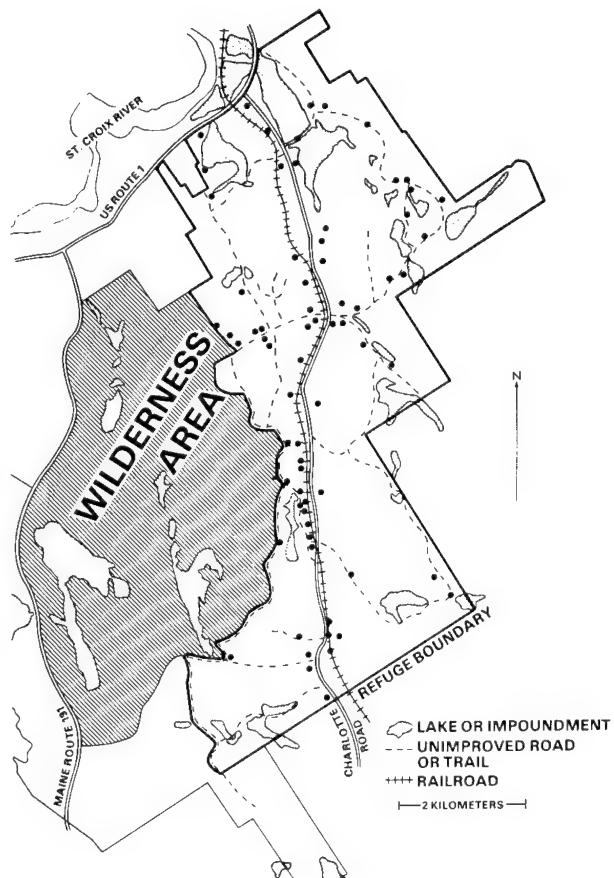


Fig. 4. Location (indicated by dots) of singing males in 1976.

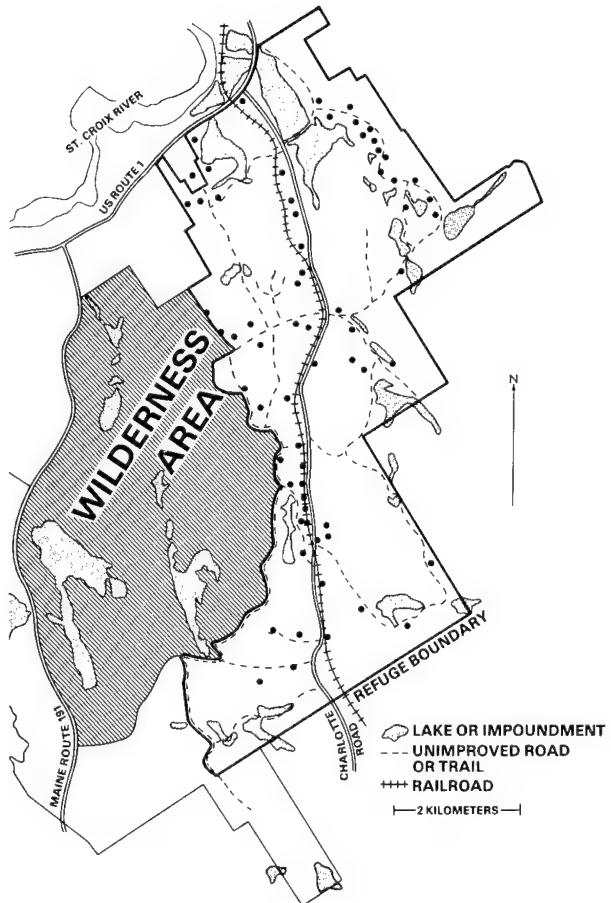


Fig. 5. Location (indicated by dots) of singing males in 1980.

There was no consistent relation between the returning number of SY females and the number of fledged young females captured the previous year (Table 15). However, the year in which the return rate was lowest (1979) was preceded by the year (1978) that had the highest number of SY breeding females and a summer drought. A previous analysis (Dwyer et al. 1982) showed slower growth rates for chicks of SY females. However, no difference in survival until fledging could be shown between broods of SY compared with ASY females (Dwyer et al. 1982).

Production

We captured 102 broods (totaling 331 chicks) during 1977-80. The number of total chick captures was considered a good index of annual production because cap-

ture effort was generally the same among years. The low number of chicks captured in 1979 indicated poor production resulting from abnormally cool and wet weather during the brood-rearing period (last week of April through May). Average daily maximum temperature was lower (14°C vs. 17°C) and total precipitation was higher (31.2 cm vs. 7.5 cm) during the last week of April and all of May of 1979 than for any other year of the study. A significant negative relation ($r = -0.985, P < 0.05, df = 2$) was found between chick production and total precipitation for this period over all 4 years but a nonsignificant negative relation ($r = -0.818, P > 0.05, df = 2$) existed between chick production and average daily maximum temperature.

Comparison of Production Indices

The annual rangewide status of the woodcock population is determined in spring and fall (Tautin et al. 1983).

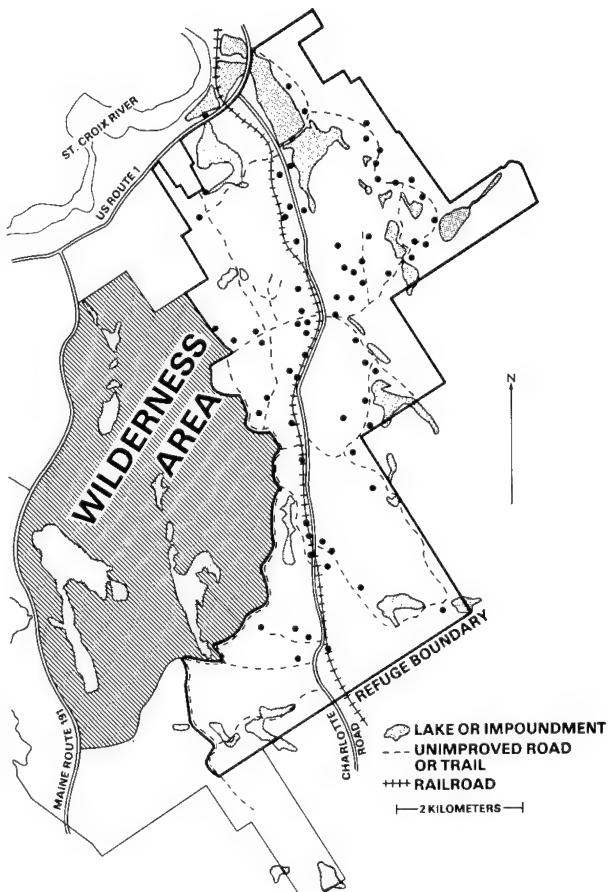


Fig. 6. Location (indicated by dots) of singing males in 1985.



Fig. 7. Banded woodcock chick before release. (Photo by G. M. Haramis).

The spring survey monitors year-to-year changes in the number of courting males heard on selected routes. The fall production survey is derived from wings solicited from hunters. From this wing sample, production indices (young per adult female) by State are determined. However, these indices may provide biased estimates of State production, because an unknown portion of each sample is composed of migrant birds. These migrants undoubtedly come from areas where climatic conditions influencing hatching success and brood survival differ radically from the area where they are shot. Thus, the wing sample represents a

collection of birds that endured different stresses during the nesting and brood-rearing period. Furthermore, neither of these surveys provides a prehunting season estimate of production. Thus, hunting season regulations are made without knowledge of production success.

We believe that there is a need to develop a technique that can indicate local production to improve local management efforts and assist in making hunting season recommendations. This technique would have to be easy to use, time efficient, and sensitive to changes in production. We examined the various capture and

Table 14. *Age ratio and number of adult woodcock caught during summer, 1977-82.*

Year	Males			Females		
	SY	ASY	ASY:SY	SY	ASY	ASY:SY
1977	14	10	0.71	23	29	1.26
1978	14	9	0.64	25	21	0.81
1979	18	11	0.61	22	27	1.23
1980	10	5	0.50	12	16	1.33
1981	8	4	0.50	16	11	0.69
1982	6	1	0.17	15	11	0.73
Total	70	40	0.57	113	115	1.02

monitoring techniques used during this study to see if any met these criteria.

We hypothesized that nightlighting selected fields and counting the number of woodcock flushed would provide an accurate index of production. To test this method we chose four major roosting fields and calculated a June through August flush rate (flushes per hectare) each year from 1977 through 1980 of 9.1, 3.3, 3.1 and 2.8, respectively. We expected a low flush rate in 1979 because there was a 33% decline in the number of chicks captured and a fourfold increase in the average precipitation during late April and the entire month of May of that year. Spring weather conditions during the other 3 years were normal. However, the flush rate declined over all 4 years. The forest management practices we were employing apparently affected woodcock use of chosen roosting areas (Sepik and Dwyer 1982) to the extent that they masked any annual variation in use.

We also compared production indices (young per adult female) obtained by using captures from night-

lighting, mist nets, and ground traps from 1976 to 1982 (Table 16). As expected, all three methods yielded low production indices in 1979. Low production indices also were noted in 1982 and corresponded with low May rainfall. Periods of little rainfall (in 1982) may result in scarce earthworm abundance leading to increased mortality of chicks. During periods of high precipitation and cool temperatures (in 1979), chick mortality may result from insufficient opportunities for foraging combined with increased chick energy requirements.

We also expected low young-to-adult female ratios in 1978 because of an extended summer drought. Sepik et al. (1982) documented some effects of the drought on our study area. None of the production indices from the three trapping techniques reflected this phenomenon (Table 16). This may be because all age and sex classes were affected similarly and, therefore, the production indices did not change. Also, the full effect of the drought was not felt until August, after many of the captures used in these indices were made.

We tested the comparability of production indices derived from the three capture methods by checking for correlation among the three techniques (Table 17). There was significant correlation between indices derived from nightlighting and ground traps and between nightlighting and mist nets ($t = 3.72$, $df = 6$, $P < 0.005$; and $t = 2.88$, $df = 6$, $P < 0.025$; Table 17). However, no significant correlation was found between indices derived from mist nets and ground traps ($t = 1.10$, $df = 6$, $P > 0.10$). Significant correlations ($r = 0.978$ and 0.916) were also found between both mist net and nightlighting production indices and the population of young estimated by the Darroch (1959) mark-recapture model ($t = 6.63$, $df = 3$, $P < 0.05$; and $t = 3.23$, $df = 3$, $P < 0.05$). On the basis of these correlations, young-to-adult female ratios derived from mist net and

Table 15. *Return rates for females first banded as fledged young the previous year on the Moosehorn National Wildlife Refuge, 1977-80.*

Year	Return rate (%)
1977	8.3 (74) ^a
1978	7.6 (105)
1979	3.9 (129)
1980	4.6 (65)
All years	6.1 (373)

^aNumber in parentheses is the number of fledged females banded the previous year.

Table 16. *Production indices^a as determined from various capture methods, 1976-82.*

Year	Capture method		
	Nightlighting	Ground traps	Mist nets
1976	7.26	10.50	17.80
1977	5.48	5.05	21.35
1978	5.40	5.07	16.80
1979	3.65	4.30	6.07
1980	4.90	5.25	10.11
1981	5.00	5.13	8.56
1982	3.28	4.31	5.50

^aYoung per adult female.

nightlighting captures are more closely related to young population estimates than are captures from ground traps. Unfortunately, all these techniques are more time consuming than simply flushing birds at night, and require highly trained personnel to catch birds and determine their age and sex.

We also compared our young-to-adult female ratios with the production estimates from the 1976-80 fall wing survey (U.S. Fish and Wildlife Service, Office of Migratory Bird Management, unpublished data). We tested wing survey results using production estimates from both the entire State of Maine and only Washington County, Maine, for (1) the entire hunting season and (2) until 10 October of the hunting season each year, for correlation with our production estimates (Table 18). There were no significant positive correlations between our estimates and the wing survey (Table 18). We did not expect good correlation with the wing survey production estimates for the entire hunting season because of the presence of migrant birds. However, we believed that early season estimates would not be biased by migrants and might correlate well with our production indices. The lack of correlation may still be due to the

presence of migrants or to errors in age and sex determination of wings during the wing survey. Numerous people are recruited each year to classify these wings by age and sex. The level of expertise varies annually, and the amount of time spent training personnel is significantly less than we found was necessary for training personnel for the banding portion of our study. We now believe that the wing survey is not an adequate predictor of local production and perhaps not even statewide production.

Nightlighting most closely met the requirements we originally set forth to predict production. Mist nets and ground traps require a greater outlay of both funds and time, and these methods limit the area that can be covered. We believe that nightlighting can be used to adequately assess production in an area each summer by locating a number of different roosting fields from which an adequate sample (75-100 woodcock) could be caught. Each field should be nightlighted at least twice monthly beginning when young birds start using the fields (about 10 June in northeastern Maine) and continuing through August. A series of sampling locations that employ standardized methodology and are situated

Table 17. *Correlation coefficients among production indices (young per adult female) derived by various trapping methods and the population estimates of young, 1976-80.*

Capture method	Ground traps	Mist nets	Young population estimate ^a
Nightlighting	0.857 ^b	0.790 ^b	0.916 ^c
Ground traps		0.478	0.593
Mist nets			0.978 ^c

^aBased on the Darroch (1959) model.

^b $P < 0.05, N = 7$

^c $P < 0.05, N = 4$

Table 18. *Correlation coefficients between production indices (young per adult female) derived from various trapping techniques and the Federal wing survey.*

Capture method and population	Production index			
	Maine (total)	Maine ^a (10 days)	Washington County (total)	Washington County ^a (10 days)
Nightlighting	-0.719 ^b	-0.195	-0.292	-0.173
Ground traps	-0.657 ^b	-0.283	-0.333	-0.335
Mist nets	-0.583	-0.494	-0.404	-0.367
Flushes per ha	-0.708	-0.828	-0.616	-0.395
Population of young	+0.070	-0.358	-0.126	-0.385

^aFirst 10 days of the season.

^b $P < 0.05$, $N = 7$.

throughout the breeding range could give a good indication of rangewide production.

Population Size

Chi-square goodness-of-fit tests were used, where possible, to determine which mark-recapture model provided the best fit for a given data set (Otis et al. 1978; Nichols et al. 1981). In some instances, however, data sets seemed to fit more than one model; our judgments were based on our knowledge of woodcock biology with respect to model assumptions. Here we present those estimates believed to be most statistically and biologically meaningful.

Population and survival estimates were computed separately for each age and sex class. Therefore, although different capture probabilities can result in different levels of precision of the estimates for the different age-sex classes, they will not affect their accuracy.

Adult Females

Recapture probabilities tended to be lower for adult females than for any other age-sex class. No estimate could be calculated for 1976 with either open or closed mark-recapture models because recapture rates from that year were too low.

Model M_t (time-specific capture probabilities) of Otis et al. (1978) best fit adult female data sets for all 4 years. There was no evidence of heterogeneity of trapping probabilities or behavioral response to trapping for any of the 4 years. The closure test in Otis et al. (1978) showed significant departure from closed population assumptions only for 1980. Estimates from the Jolly (1965) and Darroch (1959) models for the 3 years (1977-79) were not significantly different from the M_t estimates but had much larger standard errors. Model M_t estimates, in our opinion, provide the best approximation of adult female woodcock numbers (Table 19) on the study area; the number of adult females averaged 190 for 1977-80.

Table 19. *Summer population estimates for American woodcock on the Moosehorn National Wildlife Refuge, 1976-80.*

Year	Age-sex category			
	Adult female ^a	Adult male ^b	Young female ^b	Young male ^b
1976		88 ± 23	105 ± 15	263 ± 35
1977	252 ± 63 ^c	101 ± 40	215 ± 44	271 ± 43
1978	154 ± 29	104 ± 34	219 ± 36	259 ± 45
1979	127 ± 25	146 ± 24	187 ± 146	199 ± 42
1980	227 ± 90	156 ± 68	160 ± 35	254 ± 80
Mean	190 ± 29	119 ± 18	177 ± 32	249 ± 23

^aEstimates are from model M_t (time-specific capture probabilities; Otis et al. 1978).

^bEstimates are from Darroch's (1959) model allowing losses (deaths and emigration) between capture periods.

^c ± SE.

Adult Males

Recapture frequencies for adult males were sufficient to compute population estimates for all 5 years with both closed and open mark-recapture models. Closed population model runs resulted in little consistency in model selection among years. Model M_t was selected once (1979), model M_h once (1976), model M_o once (1977), and model M_b twice (1978 and 1980). Tests provided evidence of time-specific variation in capture probabilities for 1978, 1979, and 1980, behavioral variation in capture probabilities for 1977-80, and heterogeneity of capture probabilities in 1976 and 1978. This lack of consistency from closed model runs and the fact that capture interval survival rates were less than 1.0 when using open population model estimators led us to abandon the use of closed population estimators for adult males.

Goodness-of-fit tests for Jolly (1965) and Darroch (1959) models were generally inconclusive because often not enough recapture data were available for valid tests. Estimates from the Darroch (1959) model (death but no immigration) are probably most realistic for adult male woodcock on our study area (Table 19). Point estimates showed an increasing number of adult male woodcock from 1976 to 1980; male estimates increased from 88 in 1976 to 156 in 1980. Because of large variances, however, only 1976 and 1979 were significantly different (z -test, $P = 0.08$) from each other.

Young

Recapture data for young male and young female woodcock provided reasonably good data sets for population estimation. Model M_t (time-specific capture probabilities) was selected as the appropriate closed population model for 3 of 5 years for young females and 4 of 5 years for young males. Model M_o (constant probability of capture) and model M_h (heterogeneity of capture probabilities) were selected as appropriate models for females in 1979 and 1980, respectively. Model M_{tbh} (time, behavior, and heterogeneity in capture probabilities) was selected for young males in 1978. Closure tests showed significant departure from closed model assumptions in 3 of 5 years for young males and in 4 of 5 years for young females.

Open population model estimates produced somewhat lower population estimates than closed model estimates based on model M_t , but differences were not significant. Goodness-of-fit tests indicated that the Darroch (1959) model was appropriate for 3 of 5 years for young males and 2 of 5 years for young females. In

other years, data were insufficient to calculate a test statistic. Darroch's (1959) partially open model seemed to give the best overall estimates of young male and young female numbers on our study area (Table 19). Even though the average point estimate for young females for all 5 years (177) was lower than the average point estimate for young males (249), values were not significantly different.

Population Density

Singing-male surveys have been used by many authors (cf. Gregg 1984) as an index to singing-male density. Gregg (1984) found that these density estimates varied greatly, ranging from 10.4 singing grounds/100 ha in Pennsylvania and Maine (Norris et al. 1940; Mendall and Aldous 1943) to 1.7 singing grounds/100 ha in Minnesota (Godfrey 1974). He attributed these differences to a combination of habitat quality on the different areas and the methods of determining the area covered by the survey.

We calculated the singing-male density on the Moosehorn National Wildlife Refuge study area under the assumption that all the singing males in that area (3,401 ha) were counted (Table 20). This is a reasonable assumption because the survey was designed to include all possible areas where males might sing. Routes were added to the survey as new forest openings were created. We also systematically checked the study area to locate all courting males for banding purposes. This independent check was always within 10% of the survey results. With this method, density estimates ranged from a high of 2.2 singing males/100 ha in 1985 to a low of 1.3 singing males/100 ha in 1981 and 1982 (Table 20).

Mendall and Aldous (1943) conducted singing-male surveys on some of the same areas we have surveyed. Their survey included an estimated 600 ha and was limited to areas accessible by road or trail even though the interior of their study area contained suitable singing grounds. Their density estimates were conservative because only openings that harbored singing males on at least two different nights were counted as singing grounds and only those birds that both vocalized (peented) and performed courtship flights were considered to occupy an opening. The maximum density they recorded in 1939 was 10.4 singing males/100 ha. This is nearly 5 times our peak density estimate of 2.2 singing males/100 ha (Table 20). It is impossible to determine from the information presented by Mendall and Aldous (1943) to what degree their estimates are comparable with ours. It is not surprising that their

Table 20. Singing-male woodcock density based on singing-ground surveys conducted by the U.S. Fish and Wildlife Service in Maine and on the Moosehorn National Wildlife Refuge study area, 1976-85.

Year	Number of singing males on the Moosehorn study area	Number of singing males/100 ha on the Moosehorn study area ^a	Number of singing males/100 ha from the Maine survey ^b
1976	72	2.1	3.6
1977	69	2.0	2.5
1978	64	1.9	2.7
1979	67	2.0	2.6
1980	66	1.9	2.3
1981	45	1.3	2.5
1982	44	1.3	1.7
1983	58	1.7	2.3
1984	55	1.6	2.2
1985	75	2.2	2.2

^aBased on a total survey area of 3,401 ha.

^bBased on an assumed survey area of 124 ha/10-stop route.

estimates are larger, since more of the area was farmland in the early stages of abandonment when they surveyed it in 1939. Assuming that the two surveys are somewhat comparable, one realizes the potential the area has for woodcock and how the population has changed as cleared land reverted to forest.

The average number of singing males/10-stop route is reported annually for each State during the Federal rangewide survey. Gregg (1984) estimated that all singing males within a radius of 200 m of each listening point could be heard. Thus, each route would sample about 124 ha. Densities from the Maine State survey varied from a high in 1976 of 3.6 singing males/100 ha to a low in 1982 of 1.7 singing males/100 ha and were significantly greater (paired *t*-test, *t* = 4.91, *P* < 0.005, *df* = 9) than the density estimates on our study area (Table 20). Because the routes were randomly chosen, an assumption can be made that they are representative of habitat conditions and population densities through-

out the State (Tautin et al. 1983). Thus, at the beginning of the study, the study area represented poorer habitat than the State average, but as habitats were managed, singing-male densities equalled the State average by 1985.

By using the population estimates from 1977 through 1980 (Table 19), we obtained yearly summer densities of 19 to 25 birds/100 ha (Table 21). Population and density estimates indicated more adult females than adult males were present in the population in most years. These results agree with Dwyer and Nichols (1982), who found sex-specific survival differences favoring females in both adult and young age classes in the continental population.

The study area was diverse, with areas of varying habitat quality. Hardwood stands in the early stages of succession undoubtedly had high woodcock densities, whereas mature spruce-fir stands probably contained few birds. However, the study area is typical of much

Table 21. Density estimates (birds/100 ha) of various age and sex classes on the Moosehorn National Wildlife Refuge study area, 1976-80.

Year	Adult male density	Adult female density	Fledged young density	Total population density
1976	2.6		10.8	
1977	3.0	7.4	14.3	24.7
1978	3.0	4.5	14.0	21.6
1979	4.3	3.7	11.3	19.4
1980	4.6	6.7	12.2	23.4

of the reverting farmlands and forests of the Northeast. Therefore, these density estimates may serve as a baseline comparison with other areas in similar stages of forest succession.

Singing-male Surveys Versus Population Estimates

Biologists and administrators rely on singing male surveys to detect changes in continental woodcock populations (Tautin et al. 1983). Several studies have documented the existence of a surplus of nonsinging males (Sheldon 1967; Modafferi 1967; Godfrey 1974). These nonsinging males could seriously bias conclusions about population trends, depending on how variable the numbers are from year to year.

Only one study (conducted on High Island, Michigan) examined the relation between the number of adult male woodcock and the number of occupied singing grounds (Whitcomb 1974; Whitcomb and Bourgeois 1974). Unfortunately, the estimate for the adult male population size was derived in an indirect manner. Arbitrary spring-to-fall male survival rates in conjunction with estimated numbers of adult females in fall and a sex ratio derived from a sample of shot birds were used to generate the estimate. Conclusions, which showed an excellent relation between call-count surveys and adult male population levels, are thus suspect.

Singing-ground survey results (Table 22) showed a relatively stable number of active singing grounds during the 5 years in which population estimates were available. The number of displaying males ranged from a high of 72 in 1976 to a low of 64 in 1978 with a mean number of 68. Point estimates for male woodcock computed using the partially open mark-recapture model of Darroch (1959), however, showed a slowly increasing population (Table 19). Point estimates are only

significantly different between 1976 and 1979, however. A correlation coefficient computed between the number of singing grounds versus adult male population estimates resulted in $r = -0.706$ ($P = 0.390$). Singing-male surveys therefore did not accurately reflect estimated numbers of males in the population. This finding is in contrast with Whitcomb and Bourgeois (1974), who found a high correlation coefficient ($r = 0.911$) for the relation between active singing grounds and the spring male population on High Island, Michigan.

Whether call-count surveys provide a valid index to continental population change is a more difficult question. Can a call-count survey that enumerates an unknown fraction of males provide a valid index? The answer is yes, as long as the proportion of singing males to nonsinging males does not show wide annual variation over the surveyed area. The ratio of males to singing ground (Table 22) from our study was lower than in the Michigan study (Whitcomb and Bourgeois 1974) but continued to increase during 1976-80. Despite a growing male population and an increased number of forest openings, the number of singing males did not change. This substantiates our earlier contention that some males (particularly SY) remain subdominant at a singing site rather than move to a vacant opening. We believe that rapid changes in habitat could result in rapid changes in the ratio of males to singing ground. It is unlikely, however, that habitat changes are occurring rapidly over a large portion of the area covered during the annual Federal rangewide survey. Thus, results of this study do not negate the use of a call-count survey to index woodcock nationally. However, the rangewide survey is probably not very sensitive to change. Any large change in survey counts would probably be the result of some drastic change in the population.

Table 22. *Number of active singing grounds and estimated population levels of male woodcock on the Moosehorn National Wildlife Refuge study area, 1976-80.*

Year	Active singing grounds	Estimated number of adult males ^a	Adult males: singing ground
1976	72	88 \pm 23 ^b	1.2:1.0
1977	69	101 \pm 40	1.5:1.0
1978	64	104 \pm 34	1.6:1.0
1979	67	146 \pm 24	2.2:1.0
1980	66	156 \pm 68	2.4:1.0

^aPopulation estimates computed using partially open mark-recapture model of Darroch (1959).
^b \pm SE.

Unless recommendations for conducting the annual rangewide survey are followed strictly, counts can be severely biased (Tautin et al. 1983). For example, we compared total numbers of males heard singing on our study area for the 10-year period, 1976–85, with total numbers of males heard on the 12 Fish and Wildlife Service singing-ground routes in Washington and Hancock counties, Maine (Fig. 8). These counties have basically the same habitat and are subjected to the same weather patterns as our study area. About 16% of the Federal routes had missing data (i.e., surveys were not run) for specific years; in these instances, we substituted the average number of birds counted on the route over the 10-year period. Year-to-year changes in total counts of singing males on our study area and in the two surrounding counties were not always related (Fig. 8). In 1981 we noted a 32% decline in the number of singing males on our area because of an early April storm. Results from the Federal survey showed an increase in 1981 after a decline in 1980 that was not seen on our study area. By 1985 the Moosehorn counts had rebounded to the 1976 level, but the county routes had not. Overall, the Federal routes from the two counties showed no obvious pattern resulting from the severe storms in 1981 and 1982 (see "Singing Ground Availability and Use") that reduced the singing male population in our study area. Because we believe our study area counts were accurate (i.e., a special attempt was made to count all singing males on the area), we believe that differences either in the timing of census between our survey and the Federal survey or in observer quality must account for the differences.

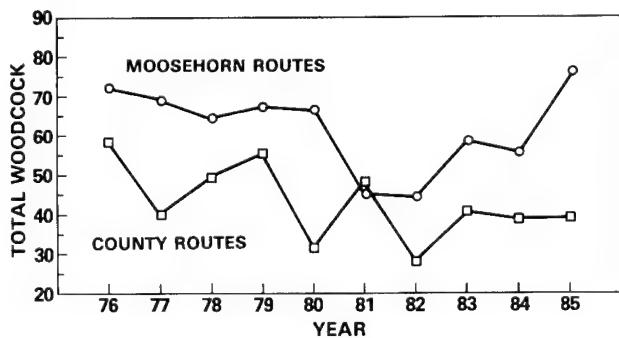


Fig. 8. Total singing-male woodcock counted during spring surveys from 1976 through 1985 on Washington County, Maine, and Moosehorn National Wildlife Refuge routes.

Survival Estimates

Brood Survival

In an earlier publication (Dwyer et al. 1982) we estimated a mortality of 0.09 chicks/day using a simple regression model of the number of chicks per brood versus brood age. Here we present a reinterpretation of these results based on regression analysis of the natural logarithm of brood size versus brood age. The slope of this regression equation provides a better estimate of the daily survival rate of chicks.

For all years (1977–80) combined, the daily survival rate was estimated at 0.9707 (SE = 0.0067). We also calculated daily survival rates for each year but could detect no significant differences between the slopes of any of the regression equations ($F = 0.552$, $df = 3, 91$, $P > 0.05$).

Woodcock chicks attain sustained flight capability at about 18 days of age according to data of Gregg (1984) and our own experience of capturing and recontacting broods. If one assumes a constant daily survival rate, an indication of the rate at which woodcock chicks survive from hatching to fledging can be calculated by $(0.9707)^{18} = 0.588$. Thus, about 59% of woodcock chicks survive the interval from hatching to fledging.

Summer Survival of Young

Sepik et al. (1983) discussed the more indirect effects of drought conditions on the woodcock population under study. Birds responded to drought in several ways: by the changing of habitats used, cessation of roosting flights, loss of weight, and delayed molt. Analysis of recapture data from young birds, using mark-recapture models, provides new information that directly relates low summer survival rates to the drought conditions.

Mean point estimates of interval survival were lowest in 1978 (Table 23). Summer 1978 was very dry; rainfall was 58% below normal (Sepik et al. 1983). Even with the large sampling variances associated with our survival estimates, the point estimate was significantly lower for 1978 than for the 1977 estimate for both young males and young females (z -test, $P = 0.07$ and $P = 0.02$, respectively). The point estimate in 1978 for young females was also significantly lower than the point estimate for 1976 (z -test, $P = 0.10$; Table 23). The point estimate for adult male summer survival rate also was the lowest in 1978 (Table 23). We are not able to show statistical significance in this situation because of large sampling variances.

From all evidence to date, we conclude that the low homing rate for SY birds in 1979 (Table 15) was the

Table 23. Mean capture interval summer survival estimates for adult male and young woodcock, 1976-79.^a

Year	Adult male	Young male	Young female
1976	0.733 ± 0.277 ^b	0.692 ± 0.109	0.798 ± 0.134
1977	0.953 ± 0.706	1.000 ± 0.239	1.000 ± 0.259
1978	0.407 ± 0.128	0.546 ± 0.196	0.483 ± 0.135
1979	0.612 ± 0.107	0.998 ± 0.245	1.000 ± 0.890
Mean	0.676 ± 0.194	0.836 ± 0.102	0.926 ± 0.237

^aBased on the Darroch (1959) model. The value for adult males is the mean of four equal interval estimates, April-August each year, whereas that for young birds is the mean of four equal interval estimates, June-August each year. Estimates that exceeded 1.0 were rounded down to 1.0.

^b± SE.

result of the lower summer survival rate of young in 1978 due to the drought. The fact that more SY females had broods that year (with concurrent slower weight gain of chicks due to inexperienced hens; Dwyer et al. 1982) probably accentuated the difference.

Woodcock Breeding Behavior

Hirons and Owen (1982) provided the most complete description of American woodcock breeding behavior and presented comparative information on the European woodcock (*Scolopax rusticola*). They characterized male American woodcock as promiscuous with a system of singing grounds analogous to dispersed leks. Oring (1982), on the other hand, considered American woodcock to exhibit male-dominance polygyny with an intermediate dispersion of display areas. One prerequisite of male-dominance polygyny is that males do not defend resources essential to females; rather, they compete for females by relative positions of dominance or by demonstrating quality through display (Oring 1982).

When the present study was initiated in 1976, the Moosehorn area had a land-use history similar to much of the northeastern United States. The lands that were clearcut around the turn of the century were covered with mature forest. High-quality woodcock habitat was restricted to the more recently abandoned farmland. The dynamics of the woodcock population on the study area were probably similar to those occurring throughout much of the Northeast. Thus, many of the population parameters estimated at the beginning of this study were those of a declining population existing in the best available habitat. The initiation of habitat improvement caused a rapid change in the use of some habitat types.

As more clearcuts were created there was a rapid shift from some types of singing grounds to the newly created openings. This was only a movement of the dominant singing-male population—the number of singing males

did not increase. The large subdominant male population did not select the newly created singing sites or the recently abandoned older sites.

This shift in singing-ground habitat use suggests that some survival or reproductive advantage was gained by dominant males using the new sites. It is unlikely that the advantage was related to food supply, because radio-marked dominant male woodcock in Pennsylvania did not use diurnal covers near singing grounds (Hudgins et al. 1985). Likewise, while searching for broods with trained bird dogs, we found few lone woodcock near singing grounds. It may be advantageous for the males to feed elsewhere because they are less likely to attract predators to the females that nest near the singing grounds (Mendall and Aldous 1943; Gregg 1984). In fact, Wrangham (1980) suggested that leks may have evolved "through active choice of passive noninterfering males." Males foraging in the vicinity of nesting females could be construed as interference.

The advantage gained by males may be one of increased survival. The longer a male survives, the greater his chance of mating. Therefore, high-quality display sites would be chosen. Gutzwiller and Wakeley (1982) found that the best singing sites were openings with shrubby growth and they postulated that these openings decreased the chance of attack by aerial predators. Although some of the clearcuts used by singing males on our study area retained some uncut shrubs, many had all shrubs and trees removed. Several males displayed on the gravel road in front of the clearcuts. We doubt that the survival of courting males was enhanced at these sites; the reason for the rapid shift in singing grounds lies elsewhere.

Hirons and Owen (1982) and Oring (1982) suggested that the lek system used by woodcock is nonresource based; the only attraction the female has to the courting area is the presence of the singing male. How then do females select males? Body size of males should

respond to sexual selection and body size in woodcock could be a determinant of male dominance. Keppie and Redmond (1985) examined male woodcock to determine if body weights were associated with the possession of a display area. They concluded that body weight did not influence the ability of a male woodcock to occupy a display area. Our data (Table 11) on weights of dominant and subdominant males support this conclusion. Male dominance seems to be strictly the result of age and experience; our data show that older, experienced males dominate display areas during the early part of the breeding season (Tables 4 and 5) when most nesting occurs (Dwyer et al. 1982). Therefore, it appears that females generally have an opportunity to select older, experienced males, but may differentiate between the quality of some resource around a display area. We believe that males have evolved the ability to determine which clearings are surrounded by the best available nesting habitat. Males obviously select certain kinds of singing grounds because we have shown a shift from certain types of openings to clearcut areas (Table 12; Fig. 3). Males that possess singing grounds surrounded by high-quality nesting habitat should have a higher probability of attracting females. We suggest that the woodcock mating system is in fact resource based; that is, it revolves around high-quality nest sites. Female behavior has evolved to use proximate habitat cues that enable females to choose males singing in high-quality nesting habitat.

Further evidence of circumstances favoring a breeding strategy more akin to a resource-defense polygyny definition can be seen by examining female nesting behavior. After mating, a female has the option of selecting the best available habitat in which to nest, but most woodcock appear to nest within 200 m of a singing ground (Mendall and Aldous 1943; Weeden 1955; Sheldon 1967; Gregg 1984). Why do females nest near singing grounds when they would seem to have the option of mating and then moving elsewhere to nest? There must be some selective advantage to nesting near the courtship arena. Breeding and nesting begin early in the spring. The chance of nest failure caused by adverse weather conditions or predation is great. Gregg (1984) found that only 50% of the nests he monitored in Wisconsin were successful. The female is also faced with the problem of finding the best male (Janetos 1980). This search takes time, and mating should not occur until a female finds a male using a singing ground surrounded by good nesting habitat. Because the chance of nest failure is great, it is to the advantage of the female to remain near the best singing area so she will not have

to invest time trying to relocate a male. Females also leave the nest during dawn and evening courtship periods, presumably to feed, but this behavior may also serve to maintain contact with the singing ground and encourage the male to continue with his courtship activities. We obtained one or two observations each year during 1976-80 of nesting females leaving their nest at dusk and flying to an adjacent singing ground.

If our hypothesis is correct, it also explains why subdominant males are present around singing grounds. If females are attracted to clearings adjacent to the better nesting cover and if renesting is common, then it would be advantageous for males to gather around these areas. Females would be less likely to mate with a male on an area surrounded by poor-quality nesting habitat. Furthermore, predation on courting males may be high. As Wittenberger (1978) reported, the use of traditional sites may lead to predator familiarity and increased predation of males. However, this disadvantage may be outweighed by the advantage gained by increased access to females. Therefore, subdominant males probably stand a good chance of eventually replacing the dominant bird. There is probably some point at which the number of subdominant males becomes too great and it is more advantageous for subdominant males to try to attract females by singing on new areas.

When poor weather conditions on our area in 1981 and 1982 eliminated one-third of the singing males, subdominant males probably suffered the same reduction. Even though subdominant males had the opportunity to take over previously held singing grounds, they found it more advantageous to maintain a subdominant role on better-quality areas. Ellingwood (1983) noted a similar trend when singing males were removed from selected singing grounds. Other males gravitated toward the better sites even though other courting areas were available.

In summary, females probably choose males at singing grounds near good nesting cover. Males on these areas are, on the average, the older, experienced birds that dominate display areas during the time when most nesting occurs. Females nest near the singing ground to eliminate the need to reassess the available singing grounds if their nest fails. To decrease predation, males have evolved a noninterfering relation with the nesting female by feeding away from the singing ground. Many males take on subdominant status because females are mainly attracted to courtship areas surrounded by the best nesting cover, predation on dominant males may be high, and remating may be common. The rapid shift of the breeding population from traditional sites to new

clearcuts on our area was probably due to the creation of openings in more suitable nesting cover.

Management Implications

Woodcock numbers in the eastern United States and Canada have been declining at a mean annual rate of 2.8% since 1966 (Tautin et al. 1983). This decline is generally attributed to a loss in habitat quality and quantity (Coulter and Baird 1982; Dwyer et al. 1983). Presumably, as habitat quality declines, food resources become less available or are poorer in quality. A lack of appropriate vegetative cover may also lead to increased predation. As the habitat base shrinks, woodcock may be forced into the best available covers at higher densities. This too may lead to increased predation, a strain on food resources and, perhaps, increased hunting pressure. Overall, survival rates will decline. This decline will be accentuated by climatic extremes such as drought, prolonged cold weather, or cool, moist conditions during the brood rearing period (Dwyer et al. 1982; Sepik et al. 1983). The maintenance and creation of high-quality singing grounds and nesting habitat is thus a prerequisite for stemming the current population decline.

The question that arises is: What is high-quality habitat? Although numerous studies have detailed habitat use by woodcock throughout its range, (see Dwyer et al. 1979 for citations) there has been no evidence to suggest what components of the habitat are currently limiting woodcock numbers. Furthermore, the measurement of habitat characteristics where woodcock are found is no guarantee that they are indicative of good woodcock habitat. They may just be a measurement of available habitat. For instance, singing-ground and nocturnal-habitat use by woodcock on our study area differed significantly from the beginning of the study to the present (Sepik and Dwyer 1982). These changes were a function of management practices. Measurement of available habitat taken at the beginning of this study would differ greatly from the same measurements taken in 1985.

Subdominant-to-dominant male capture ratios varied annually with the highest subdominant capture rate occurring in 1978 (Fig. 9). We hypothesize that a relatively low number of high-quality singing grounds were available before the large-scale habitat management program was begun. This resulted in a high-male density, competition for singing grounds, and a relatively high capture rate of subdominant males around these sites. As habitat manipulation progressed, an increasing

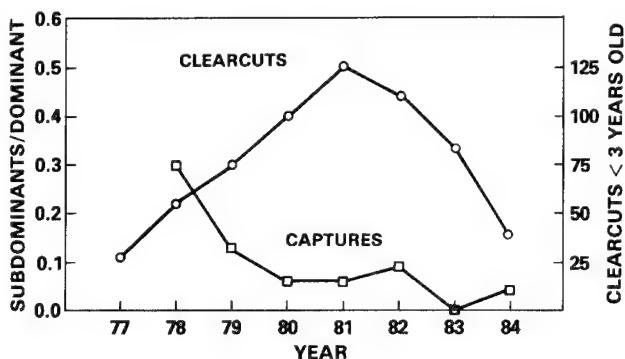


Fig. 9. Relation between subdominant and dominant male woodcock capture rates and the number of newly created clearcuts, 1977-84.

number of better-quality singing grounds became available, causing the shift in the dominant male population (Table 12). The annual decline in the subdominant-to-dominant ratio may indicate a decline in competition at singing grounds. Evidence of the attraction of the male population to the new clearcuts is found in the concurrent shift in the subdominant male capture locations. In 1978, 86% ($N = 14$) of subdominant captures occurred at nonclearcut sites, compared with 37% ($N = 19$) during 1979-82. With an increasing male population (Table 19), postmanagement (1979-84) subdominant capture rates still declined (Fig. 9), probably because subdominants were scattered over many high-quality sites rather than concentrated around a small number of high-quality sites. Eventually, without continually creating new openings, we would expect the subdominant-to-dominant male capture ratio to increase as the population continues to increase.

There is still no guarantee that we have provided optimum habitat through our management efforts. We know that we changed the type of nocturnal habitat used during the summer (Sepik and Dwyer 1982) and the type of openings used by singing males. We also have documented increases in use of managed diurnal habitat (Sepik et al. 1977), and noted a change in the size of the male population during this period. There is probably a lag time between habitat improvement and a population response. We believe the population response was even more delayed than expected because severe early spring storms depressed the male population in 1981 and 1982. By 1985 we were able to document more singing males than at the beginning of the study in 1976 (Fig. 8). The rapid movement of birds to newly created management areas suggests that these areas conferred

some advantage. If this is true, the population should continue to increase. Continued management and long-term monitoring of the population will be necessary to document this.

Even if all the public land throughout the woodcock breeding range was intensively managed for woodcock, the results would not contribute significantly toward increasing the rangewide population. There is simply not enough public land within the woodcock's range. The key to reversing woodcock habitat problems is to gain the interest of the private landowner. Coulter and Baird (1982) stated that "the current top priority is to become more broadly involved in all land-use activities and make a planned effort to reach landowners."

Woodcock management need not be sold on its own merit, but as part of a package detailing the benefits and concepts of sound wildlife management. Management for woodcock is especially pertinent to management of other early successional species such as ruffed grouse (*Bonasa umbellus*) and white-tailed deer (*Odocoileus virginianus*). Public lands can serve as demonstration areas for the dissemination of information. The Moosehorn National Wildlife Refuge has played such a role with the creation of management demonstration areas that are used to instruct both private landowners and public land managers. For those not able to visit the refuge, a booklet on woodcock management was prepared (Sepik et al. 1981) and popular articles written to maintain the public's interest. A 28-min video has also been produced for the Maine Public Broadcasting Corporation on woodcock management. Similar efforts must be started and maintained in other parts of the woodcock range if woodcock numbers are to be restored or even maintained at present levels.

Conclusions

1. Older, experienced males dominated singing grounds during the early part of the breeding season (April), whereas younger males assumed a more active role during May of each year.
2. The distribution of singing males and the pattern of use of singing grounds changed as clearcuts of varied size were created. New clearcuts not only showed the highest preferred use, but also the highest amount of sporadic use, probably because males moved from one clearcut to another among years. SY males were more apt to use newly created clearcuts; ASY males favored older clearings.
3. Environmental conditions appeared to markedly

affect local woodcock populations. A cool and wet spring resulted in poor chick production in 1979; summer drought in 1978 resulted in reduced survival of fledged young. Early spring snowstorms in 1981 and 1982 reduced the number of singing males.

4. Reasonable estimates of population size by age and sex were obtained for 1976-80. We documented a significant increase in the number of adult males in the population that we attributed to habitat management. Summer estimates ranged from 19 to 25 birds/100 ha on the study area; more adult females than adult males were present in the population in most years. Night-lighting summer roosting fields to obtain ratio of young to adult females can provide a reasonable index to production in a local area.
5. The daily survival rate of woodcock chicks in a brood was 97.1% based on a regression of the natural logarithm of brood size versus brood age. This value indicated that 58.8% of woodcock chicks survived the 18-day interval between hatching and fledging.
6. Singing-male surveys did not accurately reflect the actual number of males in the population on our study area because of an increasing subdominant (nonsinging) male population. This finding does not negate the utility of the annual rangewide call-count survey as long as there is not widespread annual variation in the ratio of males to singing grounds in surveyed areas.
7. Woodcock exhibit a polygynous, resource-based, lek mating system with females attracted to singing grounds in good nesting habitat. Thus, creation of suitable openings in managed diurnal covers is the key to woodcock habitat management. The interest of private landowners is critical to reversing woodcock habitat problems.

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A population of American woodcock (*Scolopax minor*) was studied on 3,401 ha in northeastern Maine from 1976 through 1985. Impetus for the study was the need to better describe the breeding population dynamics of woodcock and assess the effects of habitat management. Information is presented on population size, population age and sex structure, breeding male behavior, production, the relation between singing-ground surveys and actual population size, and the response of this local population to habitat management.

Key words: American woodcock, *Scolopax minor*, population, age, sex, habitat, capture methods, breeding, management, survey.

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The following is a list of recent *Fish and Wildlife Research* publications.

1. Life History and Status of the Endangered Cui-ui of Pyramid Lake, Nevada, by G. Gary Scoppettone, Mark Coleman, and Gary A. Wedemeyer. 1986. 23 pp.
2. Spread, Impact, and Control of Purple Loosestrife (*Lythrum salicaria*) in North American Wetlands, by Daniel Q. Thompson, Ronald L. Stuckey, and Edith B. Thompson. 1987. 55 pp.
3. Taxonomy, Life History, and Ecology of a Mountain Mahogany Defoliator, *Stamnodes animata* (Pearsall), in Nevada, by Malcolm M. Furniss, Douglas C. Ferguson, Kenneth W. Voget, J. Wayne Burkhardt, Arthur R. Tiedemann, and John L. Oldemeyer. In press.

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